Review of Palaeobotany and Palynology 262 (2019) 17–27

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Bamboo fossils from Oligo–Pliocene sediments of northeast India with implications on their evolutionary ecology and biogeography in Asia

Gaurav Srivastava [a,b,*], Tao Su [b], Rakesh Chandra Mehrotra [a], Pushpa Kumari [c], Uma Shankar [d]

[a] Birbal Sahni Institute of Palaeosciences, 53 University Road, Lucknow 226007, India
[b] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, CAS, Mengla 666303, China
[c] Botanical Survey of India, Central National Herbarium, Howrah 711103, India
[d] Department of Botany, North-Eastern Hill University, Shillong 793022, India

ARTICLE INFO

Article history:
Received 27 May 2018
Received in revised form 5 December 2018
Accepted 7 December 2018
Available online 11 December 2018

ABSTRACT

Bamboos comprise the subfamily Bambusoideae distributed in all continents except for Antarctica and Europe. They occupy varied habitats and are sensitive to climate change. They have sporadic flowering and low rates of dispersal, which make them indigenous and characteristic of the continents in which they occur. Plate tectonics have also played an important role in their dispersal. The dependency of various organisms on bamboos as food source and their sensitivity to climate change make bamboos difficult to manage in terms of their sustainable use. Moreover, habitat polymorphism in bamboos poses difficulties when reconstructing their evolutionary ecology, diversification, and biogeography, though molecular phylogenetic data infer their evolution in a warm and mesic environment. We report two new fossil compressions/ impressions of bamboo culms, namely *Bambusiculmus tirapensis* sp. nov. and *Bambusiculmus makumensis* sp. nov. from the late Oligocene and two new impressions of bamboo leaves, namely *Bambusium deomarense* sp. nov. and *Bambusium arunachalense* sp. nov. from the late Miocene to Pliocene sediments of northeast India. The culm fossils reported here represent the earliest records of bamboos from Asia thereby indicating that bamboos probably dispersed to Asia from India after the establishment of land connections between the Indian and Eurasian plates. The Neogene bamboos indicate the diversification of their ecological niche during the Miocene in Asia. The present fossils also reveal their adaptation to a monsoonal climate since the late Oligocene.

© 2018 Elsevier B.V. All rights reserved.

1. Introduction

The family Poaceae (grasses) envelops 12 subfamilies and among them are the Bambusoideae, which are considered to be the largest one, comprises 119 genera and ~1482 species aligned in the 3 tribes: Arundinarieae (temperate woody bamboos with 31 genera and 546 species), Bambuseae (tropical woody bamboos with 66 genera and 812 species) and Olyreae (herbaceous bamboos with 12 genera and 124 species) (Liese and Köhl, 2015). Bamboos are included in the Bambusoideae, which is indigenous to all the continents except for Antarctica and Europe and shows a latitudinal distribution between 47° S and 50°30′ N and an altitudinal occurrence from sea level to 4300 m (Soderstrom and Calderon, 1979; Judziewicz et al., 1999; Ohrnberger, 1999). The tribes Bambuseae and Arundinarieae are distributed in both the Old and New Worlds but the Olyreae, which is sister clade of Bambuseae, is restricted to the New World with a few exceptions (Hisamoto et al., 2008; Kelchner, 2013). The infrequent flowering and low dispersal rate (either by wind or animals) probably make bamboos characteristic of different continents.

According to FAO (Food and Agricultural Organisaion of the United Nations) (2010), Asia is the largest bamboo resource center in the world, where China bears highest (626) number of species (Ohrnberger, 1999) and is followed by India with 115 species (Naithani, 2008). Bamboos are also sensitive to climate change as revealed by their modern distribution and fossil records (Fig. 3). Moreover, plate tectonics might have played an important role in their dispersal in deep time (Bouchenak-Khelladi et al., 2010; Hodkinson et al., 2010). Various molecular phylogenetic studies have inferred the evolution, diversification and biogeography of the Bambusoideae (Clark, 1997; Bouchenak-Khelladi et al., 2010; Hodkinson et al., 2010; Triplett and Clark, 2010; Ruiz-Sanchez, 2011; Burke et al., 2014; Wysocki et al., 2015), however, due to polymorphism in their habitat range and disjunct distribution patterns it becomes difficult to infer their evolutionary ecology.

Fossil records of bamboos from the Paleogene as well as Neogene can provide new insights into their evolutionary ecology, diversification, and biogeography. Fossil bamboos are known from North and South America, Europe, Asia, Australia and New Zealand

* Corresponding author at: Birbal Sahni Institute of Palaeosciences, 53 University Road, Lucknow 226007, India.
E-mail address: gaurav_jan10@yahoo.co.in (G. Srivastava).

https://doi.org/10.1016/j.revpalbo.2018.12.002
0034-6667/© 2018 Elsevier B.V. All rights reserved.

(Ettingshausen, 1887a,b; Frenguelli and Parodi, 1941; Peola, 1900; Strömberg, 2004, 2005; Worobiec and Worobiec, 2005; Wang et al., 2013, 2014). Eocene bamboo fossil records are known from North and South America (Frenguelli and Parodi, 1941; Strömberg, 2004, 2005) and Australia (Ettingshausen, 1887a). In Europe, bamboos have abundant records from Neogene sediments and the earliest one is from the Oligocene of Italy (Peola, 1900), however, they are completely absent from Holocene sediments (Worobiec and Worobiec, 2005). In Asia, bamboos are known only from Neogene sediments (Wang et al., 2013, 2014).

Here, we report bamboo fossil culms and leaves from the late Oligocene and late Miocene–Pliocene (Middle Siwalik) sediments of northeast India (Fig. 1). Based on the present fossils and earlier reports from Asia we have tried to answer the following two important questions:

1. Are Asian bamboos Laurasian or Gondwanan in origin?
2. What is the evolutionary ecology of bamboos in Asia?

2. Materials and method

2.1. Fossil localities and brief geological settings

The bamboo fossils were collected from two localities in northeast India. The culm compressions/ impressions were recovered from the Tikak Parbat Formation of Barail Group of the Tirap mine, Makum Coalfield, Assam (27°17′20′′ N; 95°46′15′′ E), while the leaf impressions were unearthed from the Subansiri Formation (Middle Siwalik) of Doimara, Arunachal Pradesh (26°58′ N; 92°25.3′ E) (Fig. 2).

The Barail Group comprises three formations, the Naogaon, the Baragolai, and the Tikak Parbat in ascending stratigraphic order. The Naogaon Formation which is 1100–1700 m thick and comprises quartzitic sandstones, shales and sandy shales, is overlain by the Baragolai Formation which comprises of 300 m dominantly massive, micaceous or ferruginous sandstone (Mishra and Ghosh, 1996). The Tikak Parbat Formation is characterised by alternation of sandstones, siltstones, mudstones, shales, carbonaceous shales, clays and coal seams (Srivastava et al., 2012) (Fig. 2A). Based on the presence of a rich bivalve assemblage including *Cardiocardita* sp., *Corbicula* sp. and *Tachycardium* sp. and gastropods viz., *Mercenaria* sp., *Potomida* sp. and *Ectinochilus* sp. Misra (1983–1984) assigned an Oligocene age to similar succession exposed in the adjacent area of the Upper Assam basin. Similarly, Mandaokar (2002) also recorded Oligocene palynomorph taxa such as *Pteridacidites vermiverrucatus*Sah (1967), *Crassoretitriletes vanraadshooveniiGermeraad* et al. (1968), *Trisyncopites ramanujamii*Kar (1985) and *Bombacacidites triangulates*Kar (1985), from the Tikak Parbat Formation exposed in nearby Arunachal Pradesh. In addition, Kar et al. (1998) and Kumar et al. (2001) also recorded a similar palynoflora from the late Oligocene subsurface successions from the same study area. Moreover, based on the regional lithostratigraphy (Pascoe, 1964), remote sensing (Ganju et al., 1986) and biostratigraphy, the Tikak Parbat Formation is considered as late Oligocene in age (Raja Rao, 1981; Kumar et al., 2012). The sediments of the Barail Group represent a fluvio-marine deltaic environment. The detailed sedimentary information of the section was given by Srivastava et al. (2012), while the palynofacies were described by Kumar et al. (2012).

The Siwalik Group in Arunachal Pradesh comprises three sub-groups known as the Lower Siwalik (Dafla Formation, middle to late Miocene), Middle Siwalik (Subansiri Formation, late Miocene–Pliocene) and Upper Siwalik (Kimin Formation, late Pliocene–early Pleistocene), which are arranged in a reverse stratigraphic succession due to reverse faults (Joshi and Mehrotra, 2007) (Fig. 2B). Magnetostratigraphy data reveals that the Siwalik sediments in Arunachal Pradesh were deposited in between 13 and 2.5 Ma and the transition from Lower to Middle Siwalik is at ~10.5 Ma, while Middle to Upper Siwalik is at ~2.6 Ma (Chirouze et al., 2012). The Lower Siwalik comprising an alternation of fine to medium grained sandstone was deposited by a meandering river, while the Middle Siwalik comprising medium to coarse grained, grey, mica-rich sandstones was deposited by a braided river. The Upper Siwalik is characterised by pebble and cobble conglomerates formed as alluvial fan deposits near the mountain front (Chirouze et al., 2012).

2.2. Fossil materials and Methodology

The fossils were first cleared with the help of a soft brush and fine chisel and.

photographed under low angled natural light using Canon SX110 digital camera. The description of fossil culms and leaves is based on the terminology given by Wu (1961), Soderstrom and Young (1983), Worobiec and Worobiec (2005), Brea and Zucol (2007) and Wang et al. (2013). The modern analogs of bamboo fossils were studied in the bamboo garden of Xishuangbanna Tropical Botanical Garden, Yunnan Province, China and Botanical Survey of India, Howrah, India. It is important to mention here that one of the bamboo culm fossils was present on a big shale chunk and it was not possible to extract it, so we have provided only its photograph (Plate IV, 2; Plate V, 5).

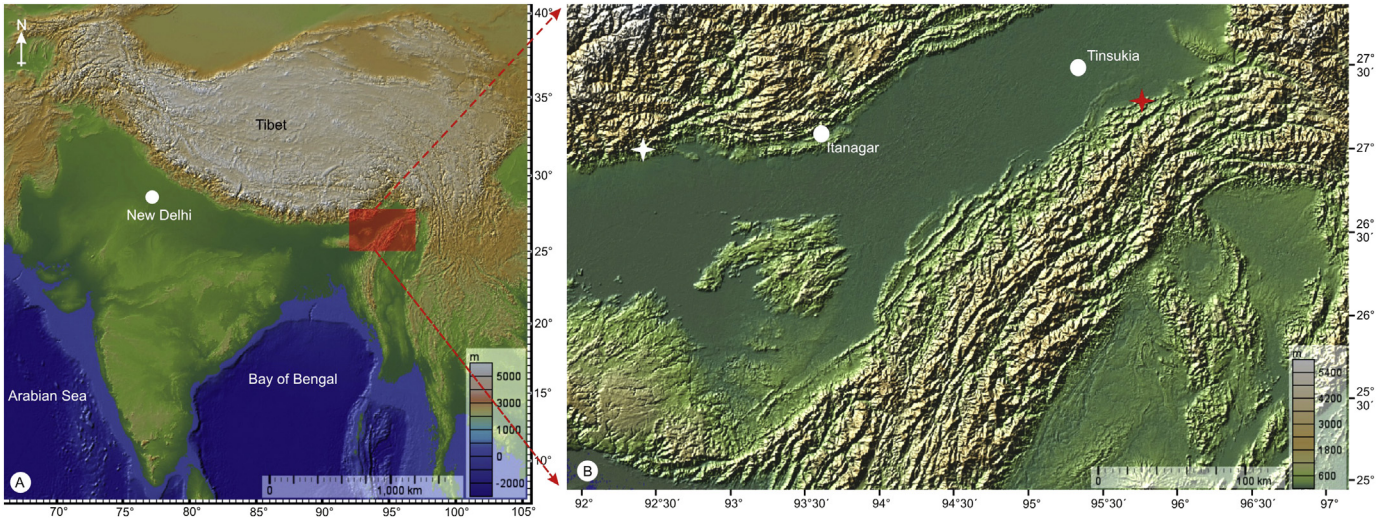

Fig. 1. Map showing the fossil locality. A: Physiographic map showing the fossil locality (red box). B: High resolution physiographic map showing the Makum Coalfield, Assam (red astrisk) and Doimara in Arunachal Pradesh (white asterisk).

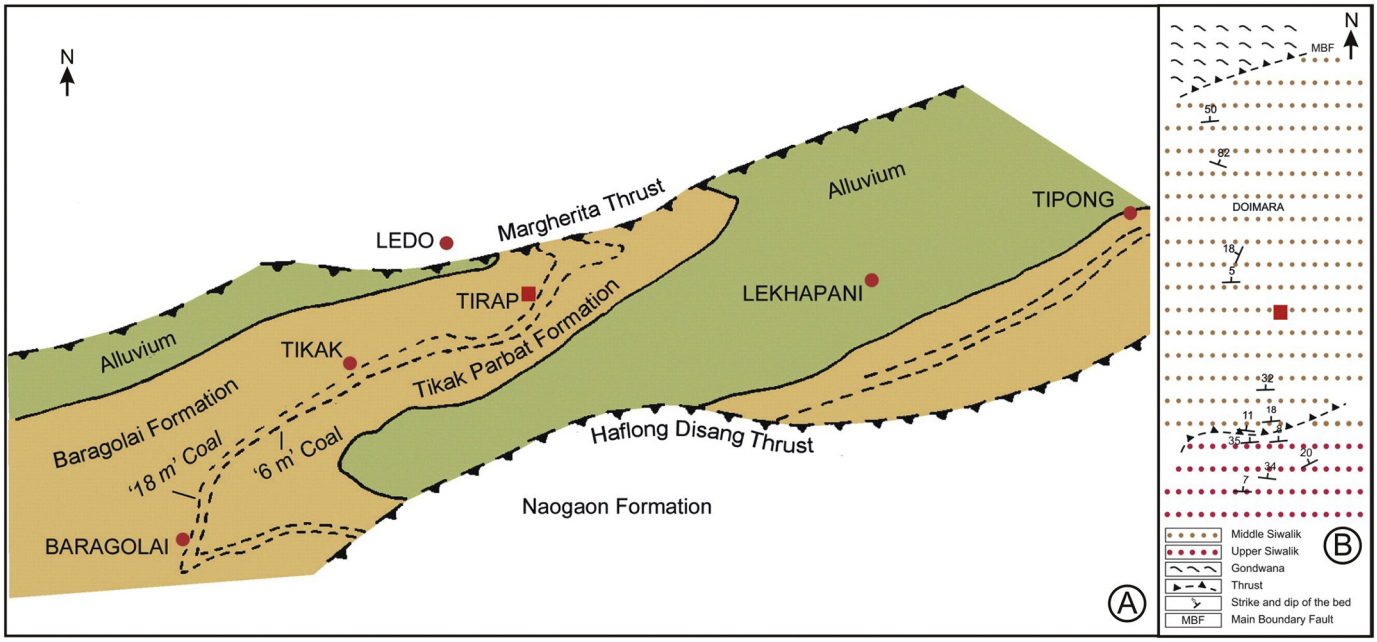

Fig. 2. Geological map of the fossil locality. A: Geological map of the Makum Coalfield, Assam showing location of the fossil locality (red square) (modified after Srivastava et al., 2012). B: Geological map of the fossil locality in West Kameng of Arunachal Pradesh (red square) (modified after Joshi and Mehrotra, 2007).

3. Results

3.1. Systematics

Order: Poales Small
Family: Poaceae Barnhart
Subfamily: Bambusoideae Luerssen.
Genus: **Bambusium** Unger 1845.

Species: *Bambusium doimaraense* G. Srivastava et R.C. Mehrotra, sp. nov.

Diagnosis: Leaf seemingly asymmetrical, linear to elongate; base cuneate; pseudopetiolate; number of 2° veins 6–7 on both sides of the midvein, 0.5–1.1 mm apart; number of 3° veins 5–7, 0.1–0.2 mm apart; transverse veins (4° veins) oriented oblique or perpendicular to 3° veins forming a tessellate venation.

Description: Leaf seemingly asymmetrical; linear, lanceolate to elongate in shape; preserved length and width of lamina 2.6–4.2 cm and 1–1.4 cm respectively; apex not preserved; base cuneate or obtuse, decurrent on pseudopetiole (Plate I, 2–4, 6); venation parallelodromous; marginal teeth on the leaf blade not observed; pseudopetiole preserved length 2.1–2.5 mm and width 1–1.1 mm; mid-vein (1° vein) distinct, 0.1–0.4 mm in thickness; less distinct lateral second-order veins (2° veins) present on both the sides of mid-vein, 6–7 in number, distance between two lateral second-order veins 0. 5–1.1 mm; delicate third-order (3°) veins present in between second-order veins, 5–7 in number, spaced 0.1–0.2 mm apart; cross (transverse/4° veins) veins connecting adjacent parallel 3° veins, oriented either slightly oblique or perpendicular to third-order veins forming a tessellate venation pattern.

Holotype: Specimen no. BSIP 41611 (Plate I, 1, 2).

Paratypes: Specimen nos. BSIP 41612 (Plate I, 3), 41,613 (Plate I, 4, 6).

Repository: Birbal Sahni Institute of Palaeosciences, Lucknow
Locality: Doimara, West Kameng District, Arunachal Pradesh
Horizon: Middle Siwalik
Age: Late Miocene to Pliocene (11.63–2.6 Ma)
Number of specimens: Three

Etymology: The specific epithet '*doimaraense*' represents the locality name from where the fossil was collected.

Species: *Bambusium arunachalense* G. Srivastava et R.C. Mehrotra, sp. nov.

Diagnosis: Leaf seemingly asymmetrical, linear to elongate; base cuneate; pseudopetiolate; number of 2° veins 10–14 on both sides of the midvein, 1–2.6 mm apart; number of 3° veins 3–9, 0.3–0.4 mm apart; transverse veins (4° veins) oriented oblique or perpendicular to 3° veins forming a tessellate venation.

Description: Leaf seemingly asymmetrical; linear, lanceolate to elongate in shape; preserved length of lamina 4.42–9.61 cm; preserved width of lamina 3.8–4.7 cm; apex not preserved; base cuneate or obtuse, decurrent on pseudopetiole (Plate II, 1); venation parallelodromous; marginal teeth on the leaf blade not observed; pseudopetiole preserved length 3.7–5.1 mm and width 3.4–3.7 mm; mid-vein (1° vein) distinct, 0.5–1.4 mm in thickness; lateral second-order veins (2° veins) less distinct, present on both the sides of mid-vein, 10–14 in number, distance between two lateral second-order veins 1–2.6 mm; third-order (3° veins) veins present in between second-order veins, parallel, faint, 3–9 in number, 0.3–0.4 mm apart; cross (transverse/ 4°) veins connecting adjacent 3° veins, oriented either slightly oblique or perpendicular to third-order veins, forming a tessellate venation pattern (Plate II, 3).

Holotype: Specimen no. BSIP 41614 (Plate II, 1)

Paratype: Specimen nos. BSIP 41615 (Plate II, 4), 41616 (Plate II, 5)

Repository: Birbal Sahni Institute of Palaeosciences, Lucknow
Locality: Doimara, West Kameng District, Arunachal Pradesh
Horizon: Middle Siwalik
Age: Late Miocene to Pliocene (11.63–2.6 Ma)
Number of specimens: Three

Etymology: The specific epithet '*arunachalense*' represents its occurrence in Arunachal Pradesh.

Affinities: The characteristic features of the fossil leaves such as linear and lanceolate to elongate leaf blades, parallelodromous and tessellate venation patterns and the presence of a pseudopetiole indicate their affinity with woody bamboos of the sub-family Bambusoideae of Poaceae (Plate I, 5, 7; Plate II, 2) (Soderstrom and Ellis, 1987; Grass Phylogeny Working Group (GPWG), 2001). A large number of genera of the Poaceae were examined in the herbarium of Central National Herbarium, Howrah, as well as consulting their virtual images available in the website of the Kew Herbarium. Leaves of *Phragmites* (subfamily

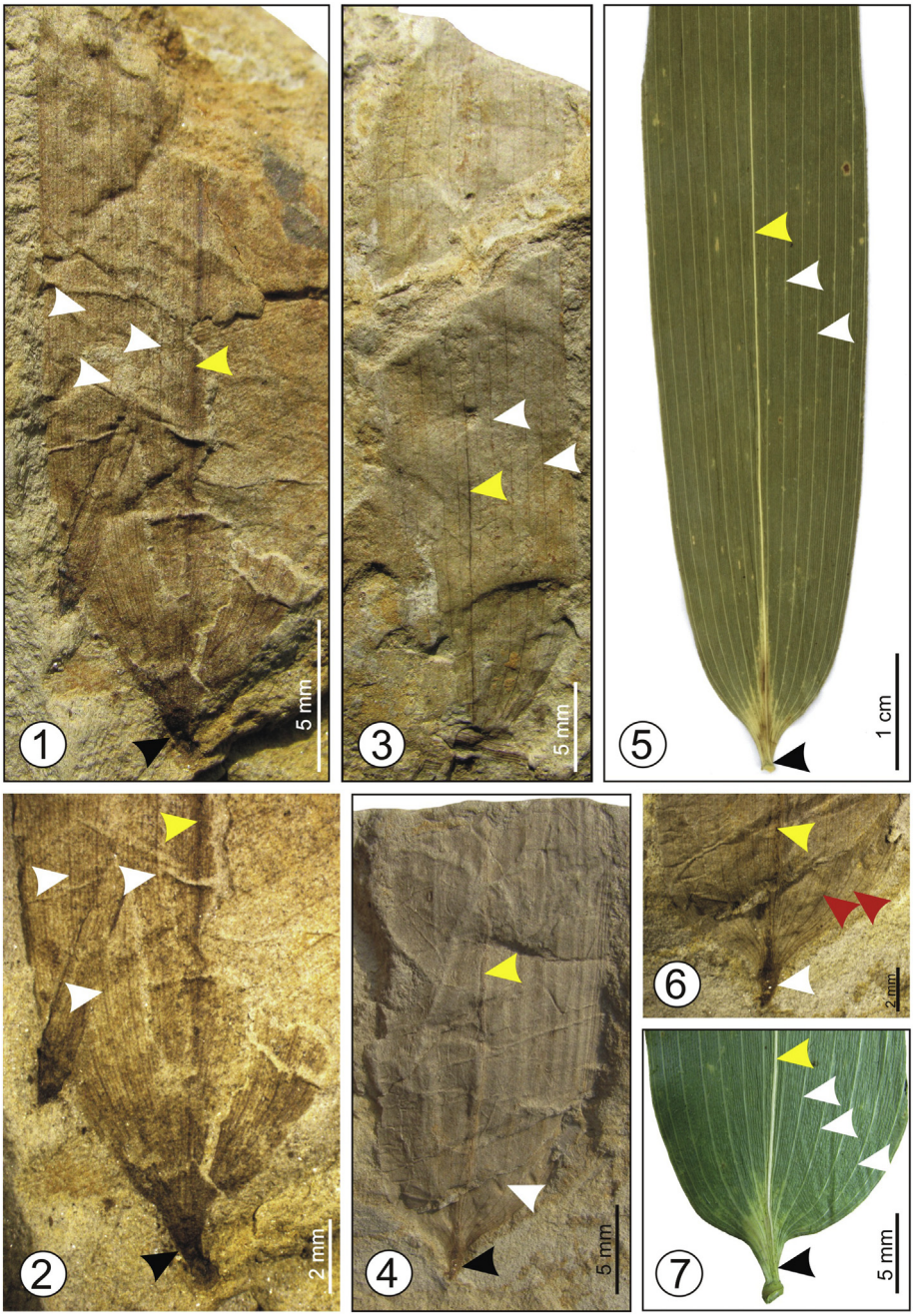

Plate I. Showing the fossil and modern leaves of bamboo. 1: *Bambusium doimarense* sp. nov. (holotype) showing shape, size, 1° vein (yellow arrow), 2° veins (white arrows) and pseudopetiole (black arrow). 2: Enlarged basal portion of *Bambusium doimarense* sp. nov. showing 1° vein (yellow arrow), 2° veins (white arrows) and pseudopetiole (black arrow). 3: *Bambusium doimarense* sp. nov. (paratype) showing shape, size, 1° vein (yellow arrow) and 2° veins (white arrows). 4: Another specimen of *Bambusium doimarense* sp. nov. showing shape, size, 1° vein (yellow arrow) and 2°vein (white arrows) and pesudopetiole (black arrow). 5: Modern leaf of bamboo (*Guadua chacoensis* Londoño and Peterson) showing similar features as in the fossil, such as 1° vein (yellow arrow) and 2° veins (white arrows) and pseudopetiole (black arrow). 6: Enlarged basal portion of the fossil leaf (Plate I, 4) showing primary vein (yellow arrow), 2° veins (red arrows) and pseudopetiole (white arrows). 7: Enlarged basal portion of the modern bamboo leaf (Plate I, 5) showing similar features as in the fossil, such as 1° vein (yellow arrow), 2° veins (white arrows) and pseudopetiole (black arrow).

Arundinoideae), *Arundo* (subfamily Arundinoideae), *Neyraudia* (subfamily Chloridoideae) and *Thysanolaena* (subfamily Panicoideae) appear close to the fossil leaves in their general shape and venation pattern, but the absence of pseudopetioles differentiates them. Though pseudopetioles are also present in other subfamilies such as Anomochlooideae, Pharoideae and Puelioideae, Ehrhartoideae, Panicoideae and Pooideae of the Poaceae (GPWG, 2001), these non-bambusoid grasses lack an abscission layer in their pseudopetioles (Sánchez-Ken and Clark, 2010); this makes it difficult to discard only the leaf blade in a similar manner as in our preserved fossil leaves.

Fossil leaves of bamboos are known from Neogene sediments of the Northern Hemisphere such as China, France, India, Italy, Japan, Nepal, Poland, Romania and Russia (Miki, 1941; Kolakovsky, 1964; Shvareva, 1970; Ozaki, 1980; Givulescu, 1984; Awasthi and Prasad, 1990; Roiron, 1991; Martinetto, 2003; Worobiec and Worobiec, 2005; Wang et al., 2013; Wang et al., 2014). The fossil leaves in our study are different from the already known fossil records in respect of a combination of characters such as the width of the leaf blade, the number of second- (2°) and third- (3°) order veins and the space between the second- and third-order veins (Table 1). Earlier described fossils such as *Bambusa ilinskiae*, *Bambusium latifolia*, *"Bambusa" lugdunensis*, *Bambusa*

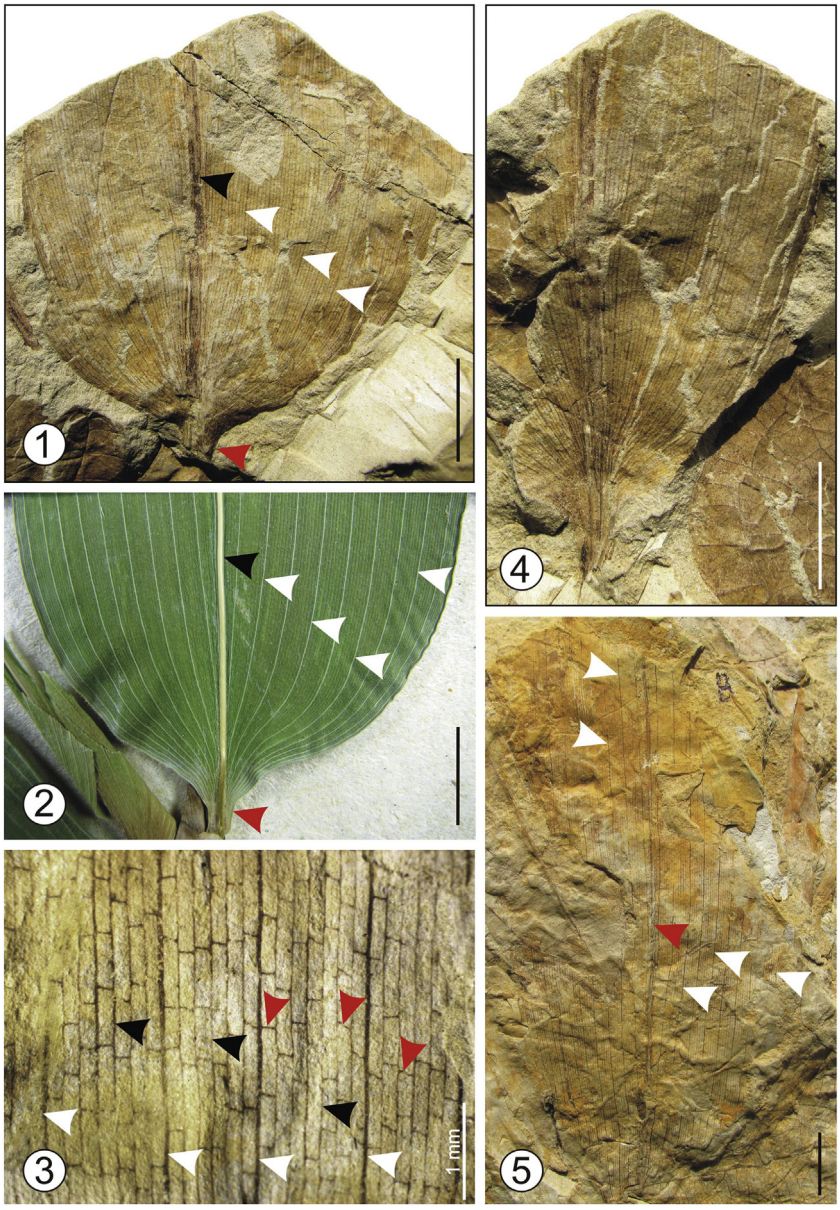

Plate II. Showing the fossil and modern leaves of bamboo. 1: *Bambusium arunachalense* sp. nov. (holotype) showing shape, size, 1° vein (black arrow) and 2° veins (white arrows) and pseudopetiole (red arrow). 2: Modern leaf of bamboo (*Dendrocalamus peculiaris* Hsueh and D.Z. Li) showing similar features as found in the fossil, such as 1° vein (black arrow), 2° veins (white arrows) and pseudopetiole (red arrow). 3: High resolution of middle portion of the fossil leaf (Plate II, 5) showing 2° veins (white arrows), 3° veins (black arrows) and transverse septa (red arrows). 4: *Bambusium arunachalense* sp. nov. (paratype) showing shape size and venation pattern. 5: Another specimen of *Bambusium arunachalense* sp. nov. showing 1° vein (red arrow) and 2° veins (white arrows) (Scale = 1 cm, unless otherwise mentioned).

sp., *Sasa kodorica*, *Bambusium* sp. A, *Bambusium* sp. B, *B. latipseudopetiolus* and *B. longipseudopetiolus* have broader leaf blade widths, which range between 14 and 55 mm. Moreover, *Bambusium angustifolia*, *"Bambusa" lugdunensis, Bambusa* sp., *Phyllostachys* sp. and *Sasa lugdunensis* have fewer (2–6) second-order veins. All these characters contrast with those of *Bambusium doimaraense* (Table 1). Fossil leaves of *Bambusa siwalika* described from various Siwalik sediments of India and Nepal (Awasthi and Prasad, 1990) are fragmentary in nature and difficult to compare with the present fossils (Table 1).

Another fossil leaf, *Bambusium arunachalense*, has a broader leaf blade width (38–47 mm) than previously described fossil leaves such as *Bambusa siwalika*, *Bambusa* sp., *Bambusium angustifolia*, *Bambusium latifolia*, *Bambusium latipseudopetiolus* and *Bambusium longipseudopetiolus*, *Bambusium* sp. B, *Sasa kodorica*, *Sasa lugdunensis* and *Phyllostachys* sp. where leaf blade widths vary in between 6 and 38 mm. Moreover, *Bambusa ilinskiae* and *Bambusa* sp. have broader leaf blades (55 mm) than *Bambusium arunachalense*. *Bambusium* sp. A shows some similarity with *B. aruanachalense*, but the former has fewer second-order veins than the latter (Table 1). The placement of fossil bamboo leaves in the context of modern generic names on the basis of morphological characters may be challenging (Soderstrom and Ellis, 1987; Worobiec and Worobiec, 2005; Wang et al., 2013), so our specimens of fossil bamboo leaves have been assigned to the already introduced leaf organ genus *Bambusium* Ünger. As the present fossil leaves are different from the already known fossils (Table 1), two new species namely, *B. doimaraense* sp. nov. and *B. arunachalense* sp. nov. are being instituted here.

Genus: **Bambusiculmus** Wang and Zhou, 2013.

Bambusiculmus tirapensis G. Srivastava et R.C. Mehrotra, sp. nov.

Specific diagnosis: Node and internode present, internode length ~5.1 cm and diameter 7.4–9.5 mm, nodal diameter 9–14 mm, striations present on the surface of the culm.

Table 1
Comparison of the present fossil leaves with the already known leaf fossil records of bamboo (modified after Li et al., 2013).

Fossil species	Leaf blade width (mm)	Second-order vein number	Third-order vein number	Lateral vein space (mm)	Third-order parallel vein space (mm)	References
Bambusa ilinskiae	55	8–10	6–10	-	-	Shvareva (1970)
Sasa kodorica	35	-	-	-	-	Kolakovsky (1964)
S. lugdunensis	6; 15	3; 5	5	-	-	Givulescu (1984)
Phyllostachys sp.	12	4–5	-	-	-	Miki (1941)
Bambusium sp. A	30–45	7–10	5–9	-	-	Ozaki (1980)
Bambusium sp. B	15–20	5–7	5–7	-	-	Ozaki (1980)
Bambusa sp.	6–12	2–4	4–6	-	-	Roiron (1991)
"Bambusa" lugdunensis	15–20	5–6?	-	-	-	Martinetto (2003)
"B." lugdunensis	8–20	4–6	5–9	1–1.5	0.15–0.2	Worobiec and Worobiec (2005)
Bambusium angustifolia	7–16	3–6	5–8	0.86–2.23	0.12–0.27	Wang et al. (2013)
B. latifoliaa	14–38	4–7	5–9	1.29–3.07	0.18–0.42	Wang et al. (2013)
Bambusa siwalika	15	7–8	-	-	-	Awasthi and Prasad (1990)
Bambusa sp.	50	-	-	0.7–0.8	-	Antal and Awasthi (1993)
Bambusa siwalika	10	-	-	2–3	-	Joshi and Mehrotra (2007)
Bambusa siwalika	13	7–8	-	-	-	Prasad (1994)
Bambusa siwalika	13–27	-	-	-	-	Guleria et al. (2000)
Bambusa siwalika	28–40	15	-	-	-	Prasad and Pradhan (1998)
Bambusium latipseudopetiolus	14–29	5–8	5–7	2.4–3.3	0.21–0.41	Wang et al. (2014)
Bambusium longipseudopetiolus	15	6	5–8	0.94–1.21	0.2–0.25	Wang et al. (2014)
Bambusium doimaraense	10–14	6–7	5–7	0.5–1.1	0.1–0.2	Present study
Bambusium arunachalense	38–47	10–14	3–9	1–2.6	0.3–0.4	Present study

Description: The specimen is a compression/impression fossil culm. Preserved length ~12 cm, bearing two distinct nodes, one complete internode and two incomplete internodes (Plate III, 1); complete internode length ~5.1 cm and diameter 7.4–9.5 mm; nodes having a diameter of 9–14 mm, nodal line (pink arrow) and a supranodal ridge present (yellow arrow) and horizontal in position; single bud present on lower portion of the culm, ~5.3 mm in diameter and ~6 mm in length (Plate III, 2); numerous scars of rootlets present on the upper boundary of the lower node (Plate III, 2); several striations present on the culm.

Holotype: Specimen no. BSIP 41617 (Plate III, 1)

Repository: Birbal Sahni Institute of Palaeosciences, Lucknow

Locality: Tirap mine, Makum Coalfield, Tinsukia District, Assam

Horizon: Tikak Parbat Formation

Age: Late Oligocene (28–23 Ma)

Number of specimens: One

Etymology: The specific epithet of the fossil '*tirapensis*' is after its occurrence in the Tirap mine of the Makum Coalfield.

Bambusiculmus makumensis G. Srivastava et R.C. Mehrotra, sp. nov. (Plate III, 3; Plate IV, 1)

Number of specimens: One

Specific diagnosis: Node and internode present, internode length ~6 cm and diameter 1.7–2.2 cm, nodal diameter 1.7–2.1 cm, striations present on the surface of the culm.

Description: The specimen is a compression/impression of fossil culm. Culm preserved length ~16.2 cm, bearing two distinct and one faint nodes, two complete internodes and two incomplete internodes (Plate IV, 1); length of two complete internodes is nearly the same i.e. ~6 cm, diameter 1.7–2.2 cm; nodes having a diameter of 1.7–2.1 cm, nodal line (yellow arrow) and supranodal ridge present (white arrow) and horizontal in position; buds not observed on the nodes; scars of rootlets not observed; several striations present on the culm.

Holotype: Specimen no. MC001 (Plate III, 3; Plate IV, 1)

Repository: Museum of the Makum Coalfield, Margherita, Tinsukia District, Assam

Locality: Tirap mine, Makum Coalfield, Assam

Horizon: Tikak Parbat Formation

Age: Late Oligocene (28–23 Ma)

Etymology: The specific epithet of the fossil '*makumensis*' represents its occurrence in the Makum Coalfield.

Affinities: The characteristic features of the fossils are distinct nodes and internodes (Plates III, IV), a characteristic nodal line, supranodal ridge, rootlets and presence of a nodal bud (Plate III, 2). All the aforesaid morphological characters undoubtedly allow the material to be assigned to the Bambusoideae of the family Poaceae. Moreover, the presence of rootlets above the nodal line in the fossil (Plate III, 2) is usually found on the lower portion in the modern *Dendrocalamus* species. Though nodal lines are also found in non-bambusoid Poaceae, yet they are always less distinct than in bamboos (Keng, 1959).

Fossil bamboo culms have been reported from several parts of the world (Fig. 3). *Chusquea* culms were reported by Berry (1929) and Frenguelli and Parodi (1941) from the Cenozoic sediments of Colombia and Eocene sediments of Argentina, respectively. However, these fossils do not bear complete information regarding details of nodal and internodal regions. The genus *Phyllostachys* sp. has been reported from the late Miocene sediments of Japan (Miki, 1941) but its culm diameter (1–1.4 cm) differs from that of the present fossils. Lakhanpal et al. (1986) reported a bamboo culm from the Lower Siwalik (middle–late Miocene) sediments of Himachal Pradesh, India having a shorter (2.5–3.5 cm) internode length than that of the present fossils. *Guadua zuloagae*, reported from the Pliocene sediments of Argentina (Brea and Zucol, 2007), was found to be different from the present fossils in having a greater (3.0–3.5 cm) internode diameter. Li et al. (2008) reported a bamboo culm having Type-I vascular bundle from the Pliocene deposits of Yunnan but without any external morphological details. Olivier et al. (2009) reported a *Guadua* fossil from the upper Pliocene–upper Pleistocene sediments of the Amazon but due to the presence of spiny or thorny structures at its nodes, it is clearly different from the present fossils. Wang et al. (2013) erected the genus *Bambusiculmus* Wang et Zhang possessing diagnostic features such as conspicuous nodes and internodes, the presence of a nodal line and horizontal or oblique supranodal ridge, remnant basal parts of the culm sheath sometimes on the nodal line and a smooth or sulcate surface. They also reported two new bamboo culm species, namely *Bambusiculmus latus* and *B. angustus* from the middle Miocene sediments of Yunnan province. *B. latus* has a greater diameter (2.5 cm), while *B. angustus* has an oblique nodal line, which is in contrast to the present fossils.

Our specimens of fossil culms show only morphological characters, and therefore their modern generic assignment is challenging (Soderstrom and Ellis, 1987; Wang et al., 2013). Under such circumstances, they are assigned to the already erected form genus *Bambusiculmus* (Wang et al., 2013). As the present fossil specimens (Plates III, 1; Plate IV, 1) have different morphological features, two new species viz., *Bambusiculmus tirapensis* sp. nov. and *Bambusiculmus makumensis* sp. nov. are being instituted here.

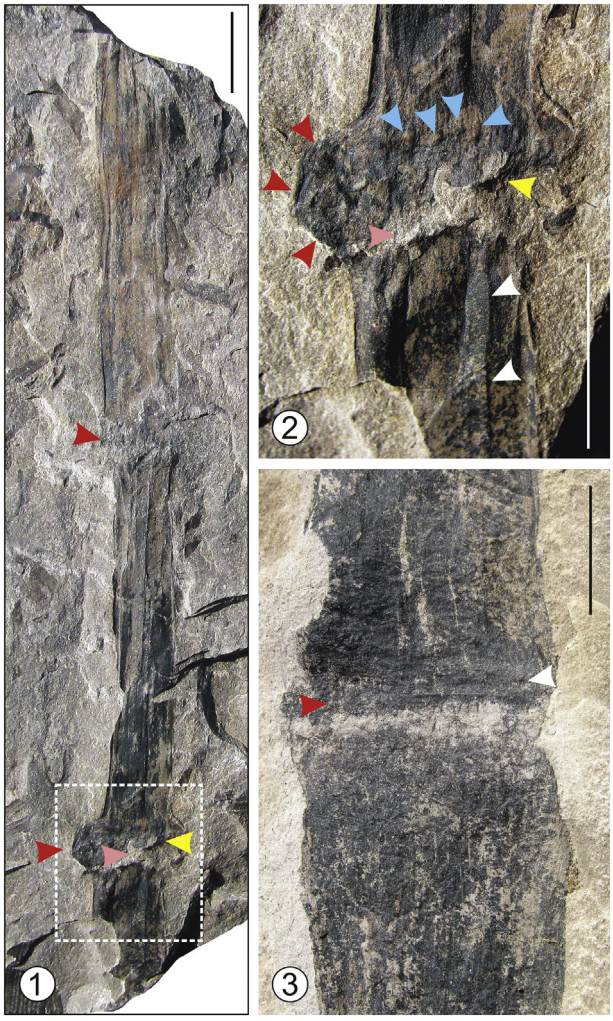

Plate III. *Bambusiculmus tirapensis* sp. nov. 1: A fossil specimen (holotype) showing shape, size, two distinct nodes (red arrows), nodal line (pink arrow) and supranodal ridge (yellow arrow). 2: High resolution image of the nodal portion of the fossil showing root lets (blue arrows), nodal bud (red arrows), nodal line (pink arrow), supranodal line (yellow arrow) and vertical striations (white arrows). 3: A nodal portion of the fossil specimen (Plate IV, 1) enlarged to show the nodal line (red arrow) and supranodal ridge (white arrow) (Scale = 1 cm).

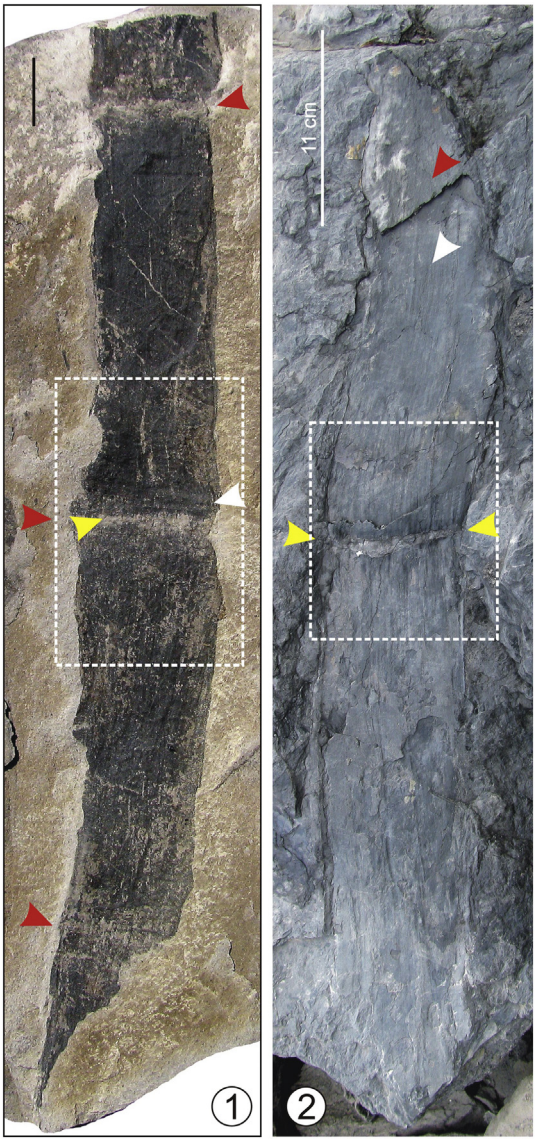

Plate IV. Bamboo fossil culms. 1. *Bambusiculmus makumensis* sp. nov. (holotype) showing morphological features with three distinct nodes (red arrows), nodal line (yellow arrow) and supranodal ridge (white arrow). 2: Another fossil culm showing node (yellow arrow), vertical fibres (white arrow) and compressed upper portion of the culm (red arrow) (Scale = 1 cm, unless otherwise mentioned).

3.2. Palaeofloristic analysis of late Oligocene and late Miocene–Pliocene floras of northeast India

The late Oligocene flora of Makum Coalfield from where the fossil bamboo culms have been recovered bears rich plant fossil records belonging to the families Equisetaceae, Podocarpaceae, Arecaceae, Anacardiaceae, Anonaceae, Burseraceae, Calophyllaceae, Clusiaceae, Combretaceae, Phyllanthaceae, Euphorbiaceae, Fabaceae, Lauraceae, Lecythidaceae, Malvaceae, Meliaceae, Memecylaceae, Myristicaceae, Rhizophoraceae and Sapindaceae (Srivastava and Mehrotra, 2013a). Based on the floristic assemblages Srivastava and Mehrotra (2013a) inferred that the late Oligocene forests were predominantly of tropical wet evergreen to moist deciduous and littoral and swampy types.

The Middle Siwalik flora from where the bamboo leaf fossils have been recorded, has yielded a large number of plant fossils whose modern analogues are *Gluta* of the Anacardiaceae, *Calophyllum* of the Calophyllaceae, *Terminalia* of the Combretaceae, *Shorea* of the Dipterocarpaceae, *Albizia*, *Cassia*, *Cynometra*, *Sindora* and *Afzelia-Intsia* of the Fabaceae, *Lindera* and *Persea* of the Lauraceae, *Ziziphus* of the Rhamnaceae, and *Euphoria* of the Sapindaceae (Mehrotra and Srivastava, 2018). All the aforesaid modern analogues indicate the existence of tropical evergreen to moist deciduous forests under warm and humid condition with plenty of rainfall. However, the numerous legumes suggest seasonal rainfall. The quantitative estimation of palaeoclimate based on the leaf morphology also reveals warm and humid condition with seasonality in the rainfall (Table 2) (Khan et al., 2014).

4. Discussion

4.1. Are Asian bamboos Laurasian or Gondwanan in origin?

The bamboo fossils have been reported from different parts of the world (Laurasia as well as Gondwana) in the form of culm, leaf, rhizome, pollen, and phytoliths (Fig. 3). The modern distribution of bamboos and the fossil records are very different in that abundant fossils have been reported from the Neogene sediments of Europe, but nowadays they are absent (Fig. 3). In this sense, bamboo fossil records provide an important insight into the geographical distributional pattern of their past population. Paleogene bamboo fossils have been reported from the Eocene of North and South America (Frenguelli and Parodi, 1941;

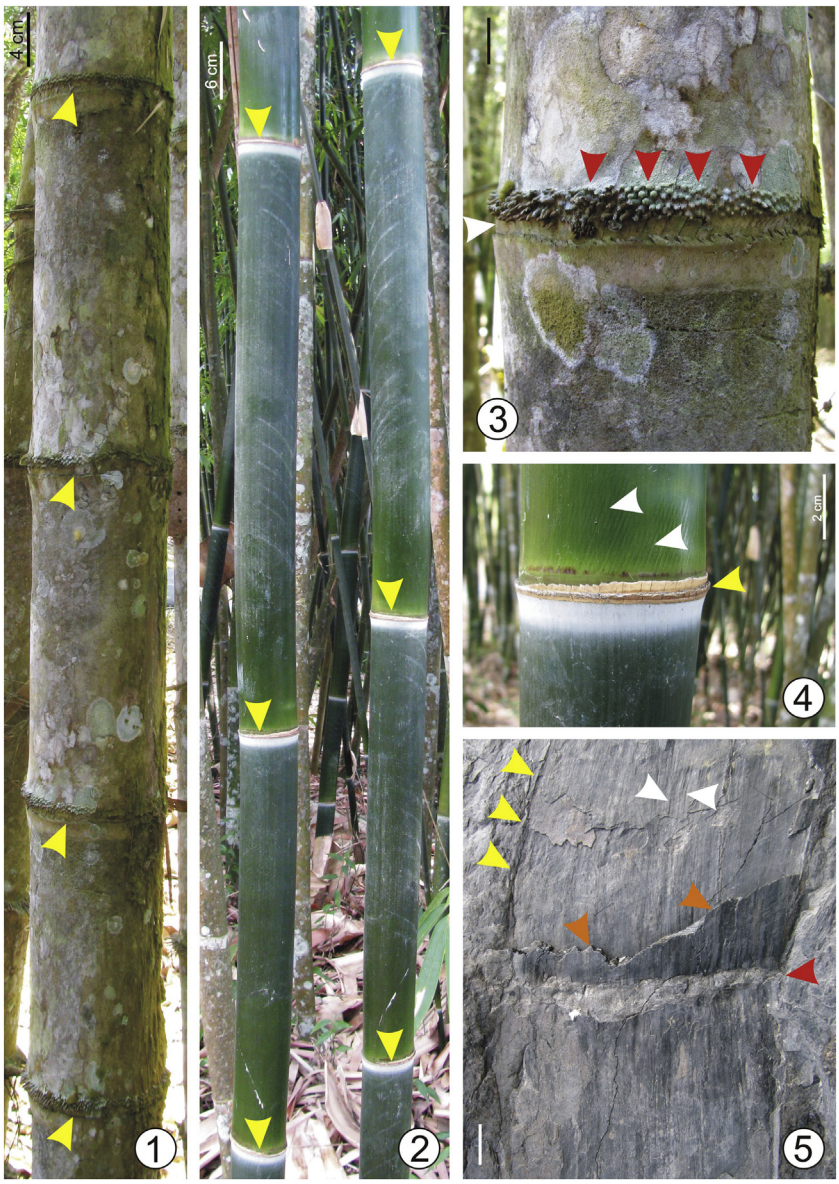

Plate V. Morphological features of modern and fossil bamboo. 1: Modern culm of *Bambusa stenoaurita* T.H. Wen showing nodes (yellow arrow) as in the fossil (Plate IV). 2: Modern culm of *Schizostachyum funghomii* McClure showing nodes (yellow arrows) as in the fossil (Plate III, 1–3; Plate IV, 1–2). 3: Enlarged portion of a node of *D. stenoauritus* showing root lets (red arrows) as in the fossil (Plate III, 2). 4: Enlarged portion of *S. funghomii* showing node (yellow arrow) and vertical fibres (white arrow) as also seen in the fossil (Plate IV, 2). 5: Enlarged culm of the fossil (Plate IV, 2) showing node (red arrow), upper compressed layer (orange arrows), margin (yellow arrows) and vertical fibres (white arrows) (Scale = 1 cm, unless otherwise mentioned).

Strömberg, 2004, 2005) and Australia (Ettingshausen, 1887a) and the Oligocene of Europe (Peola, 1900). However, during the Neogene, they occurred in Asia, Europe and North and South America. Interestingly, Africa has no fossil record, but this may be due to taphonomic filtering and rarity of paleobotanists (Fig. 3). In Asia, bamboo fossils have been reported from the Lower and Middle Siwalik (middle Miocene to Pliocene) (Lakhanpal et al., 1986; Antal and Awasthi, 1993; Prasad et al., 2004) of India, the middle Miocene (Chaney and Chuang, 1968; Wang et al., 2013), late Miocene (Li, 1984) and Pliocene (Li et al., 2008) of China, late Miocene of Nepal (Awasthi and Prasad, 1990) and Miocene sediments of Japan (Ina, 1981).

A recent report indicates that Asia is the largest bamboo resource center in the world (FAO, 2010). China harbours highest number of bamboo species (626) followed by India with 115 species (Naithani, 2008). Interestingly, ~25% of all bamboo species are found in India, particularly in the biodiversity hot-spot regions such as the Western Ghats and northeast India (Biswas, 1988; Rai and Chauhan, 1998). The present culm fossils (Plate III–IV) from the late Oligocene sediments of northeast India are the earliest occurrence of bamboos in Asia. The fossil records of bamboo in Asia indicate that bamboos most probably dispersed from India after the collision of the Indian plate with the Eurasian plate. However, more fossil records are required from Asia to validate this dispersal route because another dispersal route from Europe cannot be ruled out (Fig. 3). Many floral elements, including bamboos migrated from India to Southeast Asia and vice-versa after the late Oligocene (Bande and Prakash, 1986; Srivastava and Mehrotra, 2010, 2013a; Jacques et al., 2015). Moreover, several plant taxa migrated from India to Southeast Asia during the Neogene, such as *Bridelia* of the Phyllanthaceae, *Alphonsea* of the Anonaceae and *Semecarpus* of the Anacardiaceae (Srivastava and Mehrotra, 2012, 2013b, 2014). Clark (1997) also advocated a Gondwanan origin of bamboos based on the distribution of modern native bamboo taxa in South America. The absence of Paleogene bamboo fossils from Asia (before the discovery of present fossil) in contrast to their presence in Europe further supports that bamboos

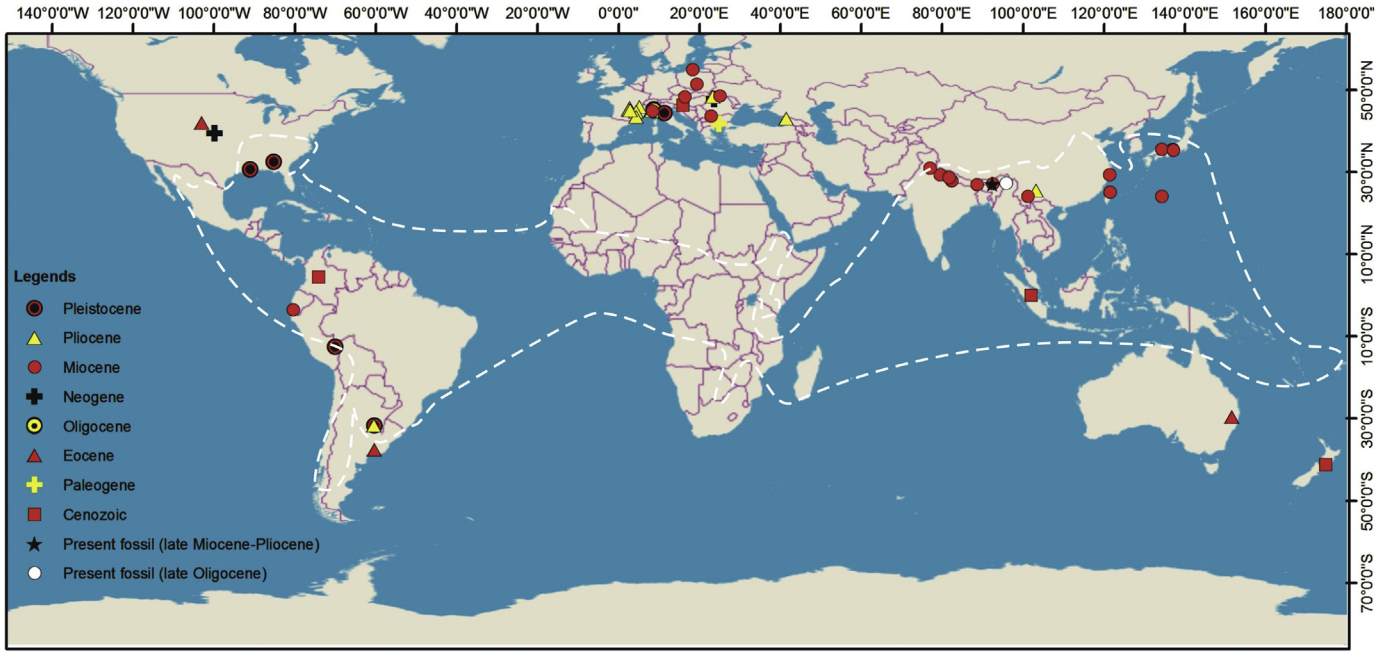

Fig. 3. Map showing the known fossil records of bamboo, present fossil localities and the modern distribution of Bambusoideae (broken line) (map source: https://www.eeob.iastate.edu/research/bamboo/maps.html).

in Asia most likely dispersed from India during the Miocene (Fig. 3), however, more Paleogene bamboo fossils are required to validate this migratory path. The molecular phylogenetic analysis also suggested that the ancestors of BEP (Bambusoideae, Ehrhartoideae, and Pooideae) clade originated in the early Eocene, while the crown node of Bambusoideae originated ~30 Ma in the middle Oligocene of Gondwanaland (Bouchenak-Khelladi et al., 2010).

4.2. What is the evolutionary ecology of bamboos in Asia?

The study of the evolutionary ecology of bamboos is important because numerous critically endangered animals, along with some humans, are directly dependant on bamboos for their food (Eronen et al., 2017). The modern climatic range of sub-family Bambusoideae is as follows: MAT (mean annual temperature) −1.1 to 27.7 °C, CMMT (cold month mean temperature) −25.8 to 27 °C, WMMT (warm month mean temperature) 19.6–33.9, MAP (mean annual precipitation) 356–10,798 mm, MPwet (mean precipitation of the wettest month) 73–2446 mm, MPdry (mean precipitation of the driest month) 0–165 mm and MPwarm (mean precipitation of the warmest month) 39–1100 mm (Utescher and Mosbrugger, 2018). However, molecular phylogenetic analysis has revealed that the Bambusoideae evolved in a closed and mesophytic environment (Bouchenak-Khelladi et al., 2010), but due to high polymorphism in their modern ecology, and contrasting fossil records beyond their modern distribution (Fig. 3) it is important to study their paleoecology and palaeoenvironment to know their environmental range in deep time.

In Asia, the fossil floras from where the bamboo fossils have been recovered are from the Siwalik of India and Nepal, middle Miocene of China and late Oligocene of India. The quantitative estimation of palaeoclimate has also been done on the aforesaid floras by the methodology such as CLAMP (Climate Leaf Analysis Multivariate Program) and CA (Coexistence Approach) analysis by various workers (Srivastava et al., 2012; Zhang et al., 2012; Khan et al., 2014). The results of the climate reconstructions are given in Table 2. It is interesting to note (Table 2) that the late Oligocene of southern Asia appears to have experienced typical tropical climate with strong seasonality in the rainfall i.e. the presence of a monsoon (wet summer and dry winter). Moreover, the Siwalik climate of India and Nepal is also tropical with seasonal rainfall. In addition, the middle Miocene climate of southern China from

Table 2
Palaeoclimate reconstructions from where the bamboo fossils have been recovered in Asia.

Climate variables	[a]Lower Siwalik (late–middle Miocene) of Darjeeling, India (Khan et al., 2014)	[a]Middle Siwalik (Pliocene) of Arunachal Pradesh, India (Khan et al., 2014)	[b]Lower Siwalik (~13–11 Ma) of Surai Khola, Nepal (Srivastava et al., 2018)	[a]Late Oligocene of Assam, India (Srivastava et al., 2012)	[b]Middle Miocene of Zhenyuan County, Yunan, China (Zhang et al., 2012)
MAT (mean annual temperature) (°C)	25.3 ± 2.8	23.6 ± 2.8	23.3 (21.1–25.4)	26.1 ± 1.4	16.1 (11.5–20.8)
CMMT (cold month temperature) (°C)	17.8 ± 4	16.9 ± 4	22.4 (20.6–24.3)	20.7 ± 2.2	2.8 (−0.2–5.9)
WMT (warm month temperature) (°C)	28.3 ± 3.4	28.1 ± 3.4	27.8 (27.5–28.1)	27.9 ± 1.7	23.3 (18.7–28)
MAP (mean annual precipitation) (mm)	-	-	2308.5 (1748–2869)	-	1091.6 (793.9–1389.4)
MPwet (wettest season rainfall) (mm)	-	-	314.5 (300–329)	-	208.8 (172.4–245.2)
MPdry (driest season rainfall) (mm)	-	-	90.5 (46–135)	-	13.9 (5.7–22.1)
GSP (mm)	2423.3 ± 916.2	1981.2 ± 91.6	-	2460 ± 307	
3-WET (mm)	1117.3 ± 528	994.1 ± 528	-	1381 ± 173	
3-DRY (mm)	288.6 ± 115	137.8 ± 115	-	67 ± 42	

[a] CLAMP (Climate Leaf Analysis Multivariate Program) methodology has been used for the palaeoclimate reconstruction.
[b] CA (Coexistence Approach) methodology has been used for the palaeoclimate reconstruction.

where bamboo fossils have been reported experienced a cool climate with strong seasonality in the rainfall. The data in Table 2 indicates that the late Oligocene bamboos were growing in a warm and humid condition as also depicted by the molecular data (Bouchenak-Khelladi et al., 2010). However, during the Miocene they probably broadened their ecological niche and adapted to cooler climates (Table 2) as observed in the Miocene of China. Interestingly, one thing common to all the geological horizons is the ability of bamboos to survive in monsoonal climates since the late Oligocene (Table 2). So from fossil records and the aforesaid discussion, it is clear that in Asia the ancient bamboos probably evolved in a tropical monsoon type of ecosystem having a warm and humid climate, however, more fossils and quantitative palaeoclimate data are needed to strengthen these inferences.

5. Conclusions

Here, we report fossil leaves and culms of bamboo from the late Miocene–Pliocene (Middle Siwalik) sediments of Arunachal Pradesh and late Oligocene sediments of Assam. The culm fossils are the earliest record of bamboos from Asia and suggest that bamboos migrated to Asia from India after closure of the ocean between India and Eurasia. The fossil records of bamboos also indicate that ancient bamboos diversified in warm and humid monsoonal climates in Asia.

Acknowledgements

GS and RCM are thankful to the Director of Birbal Sahni Institute of Palaeosciences, Lucknow for permission to publish this work. Thanks are also due to the Director, Central National Herbarium, Howrah and the Authorities of the Makum Coalfield, Margherita for granting permission to work. The present research was supported by in-house BSIP project number 2.11, Chinese Academy of Sciences President's International Fellowship Initiative (reference number 2018VMC0005) awarded to GS and Key Research Program of Frontier Sciences, CAS (reference number QYZDB-SSW-SMC016) to TS. Authors are thankful to Dr. Lutz Kunzmann, Prof. R.A. Spicer and Prof. Zhekun Zhou for their valuable comments and suggestions. US acknowledges the support under INSA-CAS Bilateral Exchange Programme 2018 and facilities availed at the North-Eastern Hill University, Shillong for his studies on biodiversity of forests of northeast India.

References

Antal, J.S., Awasthi, N., 1993. Fossil flora from the Himalayan foot-hills of Darjeeling District, West Bengal and its palaeoecological and phytogeographical significance. Palaeobotanist 42, 14–60.
Awasthi, N., Prasad, M., 1990. Siwalik plant fossils from Surai Khola area, Western Nepal. Palaeobotanist 38, 298–318.
Bande, M.B., Prakash, U., 1986. The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-Malayan region. Rev. Palaeobot. Palynol. 49, 203–233.
Berry, E.W., 1929. Tertiary fossil plants from Colombia, South America. Proc. United States Natl. Museum 75, 1–12.
Biswas, S., 1988. Studies on bamboo distribution in North-eastern region of India. Ind. For. 114, 514–531.
Bouchenak-Khelladi, Y., Verboom, G.A., Savolainen, V., Hodkinson, T.R., 2010. Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. Bot. J. Linn. Soc. 162, 543–557.
Brea, M., Zucol, A.F., 2007. *Guadua zuloagae* sp. nov., the first petrified bamboo culm record from the Ituzaingó Formation (Pliocene), Paraná Basin, Argentina. Ann. Bot. 100, 711–723.
Burke, S.V., Clark, L.G., Triplett, J.K., Grennan, C.P., Duvall, M.R., 2014. Biogeography and phylogenomics of new world Bambusoideae (Poaceae), revisited. Am. J. Bot. 101, 886–891.
Chaney, R.W., Chuang, C.C., 1968. An oak-laurel forest in the Miocene of Taiwan (Part 1). Proc. Geol. Soc. China 11, 3–18.
Chirouze, F., Dupont-Nivet, G., Huyghe, P., van der Beek, P., Chakraborti, T., Bernet, M., Erens, V., 2012. Magnetostratigraphy of the Neogene Siwalik Group in the far eastern Himalaya: Kameng section, Arunachal Pradesh, India. J. Asian Earth Sci. 44, 117–135.
Clark, L.G., 1997. Bamboos: The centerpiece of the grass family. In: Chapman, G.P. (Ed.), The Bamboos. Academic Press, London, UK.
Eronen, J.T., Zohdy, S., Evans, A.R., Tecot, S.R., Wright, P.C., Jernvall, J., 2017. Feeding ecology and morphology make a bamboo specialist vulnerable to climate change. Curr. Biol. 27, 1–6.
Ettingshausen, C.R., 1887a. Beiträge zur Kenntniss der Tertiärflora Australiens. Denkschr. K. Ak. Wiss. 53, 81–142.
Ettingshausen, C.R., 1887b. Beiträge zur Kenntniss der fossilen Flora Neuseelands. Denkschr. K. Ak. Wiss. 53, 143–192.
FAO, 2010. Food and Agriculture Organization of the United Nations. Global Forest Resources Assessment . Main Report. FAO Forestry Paper 163. FAO, Rome.
Frenguelli, J., Parodi, L.R., 1941. Una *Chusquea* fósil de El Mirador (Chubut). Notas del Museo de La Plata Tomo 6. Paléo 32, 235–238.
Ganju, J.I., Khare, B.M., Chaturvedi, J.S., 1986. Geology and hydrocarbon prospects of Naga Hills south of 27° latitude. Bull. Oil Nat. Gas Comm. 23, 129–145.
Germeraad, J.H., Hopping, C.A., Muller, J., 1968. Palynology of tertiary sediments from tropical areas. Rev. Palaeob.Palynol. 6, 189–348.
Givulescu, R., 1984. Die fossile flora des Fundortes Chiuzbaia "H" (Kreis Maramures, Rumänien). Dari de Seama ale sedintelor. Institutul de Geologie si Geofizica Paleontologie 69, 69–93.
Grass Phylogeny Working Group (GPWG), 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). Ann. Miss. Bot. Gard. 88, 373–457.
Guleria, J.S., Srivastava, Rashmi, Prasad, M., 2000. Some fossil leaves from the Kasauli Formation of Himachal Pradesh, North-West India. Himal. Geol. 21, 43–52.
Hisamoto, Y., Kashiwagi, H., Kobayashi, M., 2008. Use of flowering gene *FLOWERING LOCUS T (FT)* homologs in the phylogenetic analysis of bambusoid and early diverging grasses. J. Plant Res. 121, 451–461.
Hodkinson, T.R., Chonghaile, G.N., Sungkaew, S., Chase, M.W., Salamin, N., Stapleton, C.M.A., 2010. Phylogenetic analyses of plastid and nuclear DNA sequences indicate a rapid late Miocene radiation of the temperate bamboo tribe Arundinarieae (Poaceae, Bambusoideae). Plant Ecol. Divers. 3, 109–120.
Ina, H., 1981. Miocene fossils of the Mizunami group, central Japan. Monogr. Mizunami Fossil Mus. 2, pp. 1–20.
Jacques, F.M.B., Shi, G.L., Su, T., Zhou, Z.K., 2015. A tropical forest of the middle Miocene of Fujian (SE China) reveals Sino-Indian biogeographic affinities. Rev. Palaeobot. Palynol. 216, 76–91.
Joshi, A., Mehrotra, R.C., 2007. Megaremains from the Siwalik sediments of West and East Kameng districts, Arunachal Pradesh. J. Geol. Soc. India 69, 1256–1266.
Judziewicz, E.J., Clark, L.G., Londoño, X., Stern, M.J., 1999. American Bamboos. Smithsonian Institution, Washington, DC.
Kar, R.K., 1985. The fossil flora of Kachcha-IV, Tertiary Palynostratigraphy. Palaeobotanist 34, 1–280.
Kar, R.K., Handique, G.K., Kalita, C.K., Mandal, J., Sarkar, S., Kumar, M., Gupta, A., 1998. Palynostratigraphical studies on subsurface Tertiary sediments in Upper Assam Basin, India. Palaeobotanist 42, 183–198.
Kelchner, S.A., 2013. Higher level phylogenetic relationships within the bamboos (Poaceae: Bambusoideae) based on five plastid markers. Mol. Phylogenet. Evol. 67, 404–413.
Keng, Y.L., 1959. Flora Illustralis Plantarum Primarum Sinicarum — Gramineae. Science Press, Beijing (in Chinese).
Khan, M.A., Spicer, R.A., Bera, S., Ghosh, R., Yang, J., Spicer, T.E.V., Guo, S.X., Su, T., Jacques, F.M.B., Grote, P.J., 2014. Miocene to Pleistocene floras and climate of the Eastern Himalayan Siwaliks, and new palaeoelevation estimates for the Namling–Oiyug Basin, Tibet. Global Planet. Change 113, 1–10.
Kolakovsky, A.A., 1964. Pliotsenovaya flora Kodora (A Pliocene flora of the Kodor River). Sukhumskii Botanicheskii Sad Monografii 1, 1–209 (in Russian).
Kumar, M., Mandal, J.P., Dutta, S.K., Bhuyan, D., Das, B., Saikia, B., 2001. Palynostratigraphy of the subsurface sediments of Upper Assam basin, India. Geobios 34 (3), 241–251.
Kumar, M., Srivastava, G., Spicer, R.A., Spicer, T.E.V., Mehrotra, R.C., Mehrotra, N.C., 2012. Sedimentology, palynostratigraphy and palynofacies of the late Oligocene Makum Coalfield, Assam, India: a window on lowland tropical vegetation during the most recent episode of significant global warmth. Palaeogeogr. Palaeoclimatol. Palaeoecol. 342–343, 143–162.
Lakhanpal, R.N., Tewari, A.P., Guleria, J.S., 1986. Occurrence of bamboo in the Siwalik beds near Ranital. 35. Palaeobotanist, Himachal Pradesh, pp. 184–186.
Li, C.S., Yi, T.M., Yao, Y.F., 2008. Vegetation succession and environment change in China. Late Cenozoic Plants and Climates in Yunnan. vol. 1. Phoenix Publishing & Media, INC, Jiangsu Science & Technology Press, Nanjing in Chinese, with English Summary.
Li, H.M., 1984. Neogene flora from eastern Zhejiang, China. In: Whyte, R.O. (Ed.), The Evolution of the East Asia Environment. Palaeobotany, Palaeozoology and Palaeanthropology. 2. Centre of Asian Studies, University of Hong Kong, Hong Kong, pp. 461–466.
Liese, M., Köhl, M., 2015. Bamboos: The Plant and its Uses. Springer International Publishing, Switzerland.
Mandaokar, B.D., 2002. Palynofloral investigation of the Tikak Parbat Formation (Late Oligocene) of Borjan area, Nagaland, India. Minetech 23, 19–23.
Martinetto, E., 2003. Leaves of terrestrial plants from the Pliocene shallow marine and transitional deposits of Asti (Piedmont NW Italy). B. Soc. Paleontol. Ital. 42, 75–111.
Mehrotra, R.C., Srivastava, G., 2018. Neogene flora of Arunachal Himalaya. In: Das, A.P., Bera, S. (Eds.), Plant diversity in the Himalaya hot spot region. Bishen Singh Mahendra Pal Singh, Dehradun, pp. 399–412.
Miki, S., 1941. On the change of flora in eastern Asia since Tertiary Period (I). The clay or lignite beds in Japan with special reference to the *Pinus trifolia* beds in Central Hondo. Jpn. J. Bot. 11, 237–303.
Mishra, H.K., Ghosh, R.K., 1996. Geology, petrology and utilization of some Tertiary coals of the northeastern region of India. Int. J. Coal Geol. 30, 65–100.
Misra, U.K., 1983-1984. Palaeontological studies of Disang and Barail sedimentaries in a part of Manipur East. Unpublished GSI Progess Report cited in: recent advances in

the study of Tertiary stratigraphy of Northeast India—a critical resume. Geol. Surv. India Spl. Publ 23, 1–25.
Naithani, H.B., 2008. Diversity of Indian bamboos with special reference to North-east India. Ind. For. 134, 765–788.
Ohrnberger, D., 1999. The Bamboos of the World: Annotated Nomenclature and Literature of the Species and the Higher and Lower Taxa. Elsevier, Amsterdam.
Olivier, J., Otto, T., Roddaz, M., Antoine, P.-O., Londono, X., Clark, L.G., 2009. First macrofossil evidence of a pre-Holocene thorny bamboo cf. *Guadua* (Poaceae: Bambusoideae: Bambuseae: Guaduinae) in South-Western Amazonia (Madre de Dios — Peru). Rev. Palaeobot. Palynol. 153, 1–7.
Ozaki, K., 1980. Late Miocene Tatsumitoge flora of Tottori Prefecture, Southwest Honshu, Japan (III). Sci. Rep. Yokohama Nat. Univ. Sect. I. Math. Phys. Chem. 2, 19–45.
Pascoe, E.H., 1964. A Manual of the Geology of India and Burma 3. Government of India Press, Calcutta.
Peola, P., 1900. Flora Tongriana di Pavone d'Alessandria. Boll. Soc. Geol. Ital. 19, 36–62.
Prasad, M., 1994. Siwalik (Middle Miocene) leaf impressions from the foot-hills of Himalayas, India. Tert. Res. 15, 53–90.
Prasad, M., Pradhan, U.M.S., 1998. Study of plant fossils from the Siwalik sediments of Far Western Nepal. Palaeobotanist 47, 99–109.
Prasad, M., Ghosh, R., Tripathi, P.P., 2004. Floristics and climate during the Siwalik (middle Miocene) near Kathgodam in the Himalayan foot hills of Uttaranchal, India. J. Palaeontol. Soc. India 49, 35–93.
Rai, S.N., Chauhan, K.V.S., 1998. Distribution and growing stock of bamboos in India. Ind. For. 124, 89–97.
Raja Rao, C.S., 1981. Coalfields of India; coalfields of northeastern India. Bull. Geol. Sur. India, Series A 45, 1–76.
Roiron, P., 1991. Les macroflores d'âge Miocène Supérieur des diatomites de Murat (Cantal France). Implications paléoclimatiques. Palaeontogr. B 223, 169–203.
Ruiz-Sanchez, E., 2011. Biogeography and divergence time estimates of woody bamboos: insights in the evolution of Neotropical bamboos. Bol. Soc. Bot. Méx. 88, 67–75.
Sah, S.C.D., 1967. Palynology of an Upper Neogene profile from Rusizi valley (Burundi). Musée Royal de l'Afrique Centrale Série 8, 1–173.
Sánchez-Ken, J.G., Clark, L.G., 2010. Phylogeny and a new tribal classification of the Panicoideae s.l. (Poaceae) based on plastid and nuclear sequence data and structural data. Am. J. Bot. 97, 1732–1748.
Shvareva, N.Y., 1970. Miotsenovaya flora Pistynki v Predkarpat'e (The Miocene flora of Pistynka (Cis-Carpathian Area)). Bot. Zentr. 55, 443–456 in Russian.
Soderstrom, T.R., Calderon, C.E., 1979. Ecology and phytosociology of bamboo vegetation. In: Numata, M. (Ed.), Ecology of Grasslands and Bamboolands in the World. W. Junk bv Publishers, Netherland.
Soderstrom, T.R., Ellis, R.P., 1987. The position of bamboo genera and allies in a system of grass classification. In: Soderstrom, T.R., Hilu, K.W., Campbell, C.S., Barkworth, M.E. (Eds.), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C., London.
Soderstrom, T.R., Young, S.M., 1983. A guide to collecting bamboos. Ann. Miss. Bot. Gard. 70, 128–136.
Srivastava, G., Mehrotra, R.C., 2010. Tertiary flora of northeast India vis-à-vis movement of the Indian plate. Mem. Geol. Soc. India 75, 123–130.
Srivastava, G., Mehrotra, R.C., 2012. The oldest fossil of *Semecarpus* L.f. from the Makum Coalfield, Assam, India and comments on its origin. Curr. Sci. 102, 398–400.
Srivastava, Gaurav, Mehrotra, R.C., 2013a. Low latitude floral assemblage from the Late Oligocene sediments of Assam and its palaeoclimatic and palaeogeographic significance. Chinese Sci. Bull. (Suppl. I), 156–161.
Srivastava, Gaurav, Mehrotra, R.C., 2013b. First fossil record of *Alphonsea* Hk. f. & T. (Annonaceae) from the late Oligocene sediments of Assam, India and comments on its phytogeography. PLoS One 8, e53177.
Srivastava, Gaurav, Mehrotra, R.C., 2014. Phytogeographical implication of *Bridelia* Will. (Phyllanthaceae) fossil leaf from the late Oligocene of India. PLoS One 9, e111140.
Srivastava, G., Spicer, R.A., Spicer, T.E.V., Yang, J., Kumar, M., Mehrotra, R.C., Mehrotra, N.C., 2012. Megaflora and palaeoclimate of a late Oligocene tropical delta, Makum Coalfield, Assam: evidence for the early development of the south Asia monsoon. Palaeogeogr. Palaeoclimatol. Palaeoecol. 342 (343), 130–142.
Srivastava, G., Paudayal, K.M., Utescher, T., Mehrotra, R.C., 2018. Miocene vegetation shift and climate change: evidence from the Siwalik of Nepal. Glob. Planet. Change 161, 108–120.
Strömberg, C.A.E., 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 239–275.
Strömberg, C.A.E., 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. Proc. Natl. Acad. Sci. U. S. A. 102, 11980–11984.
Triplett, J.K., Clark, L.G., 2010. Phylogeny of the temperate woody bamboos (Poaceae: Bambusoideae) with an emphasis on *Arundinaria* and allies. Syst. Bot. 35, 102–120.
Utescher, T., Mosbrugger, V., 2018. The Palaeoflora Database. http://www.palaeoflora.de.
Wang, L., Jacques, F.M.B., Su, T., Xing, Y.W., Zhang, S.T., Zhou, Z.K., 2013. The earliest fossil bamboos of China (middle Miocene, Yunnan) and their biogeographical importance. Rev. Palaeobot. Palynol. 197, 253–265.
Wang, Q., Ma, F., Yang, Y., Dong, J., Wang, H., Li, R., Xu, X., Sun, B.N., 2014. Bamboo leaf and pollen fossils from the late Miocene of eastern Zhejiang, China and their phytogeographical significance. Acta Geol. Sin. 88, 1066–1083.
Worobiec, E., Worobiec, G., 2005. Leaves and pollen of bamboos from the Polish Neogene. Rev. Palaeobot. Palynol. 133, 39–50.
Wu, M.C., 1961. The classification of Bambuseae based on leaf anatomy. Bot. Bull. Acad. Sin. 3, 83–114.
Wysocki, W.P., Clark, L.G., Attigala, L., Ruiz-Sanchez, E., Duvall, M.R., 2015. Evolution of the bamboos (Bambusoideae; Poaceae): a full plastome phylogenomic analysis. BMC Evol. Biol. 15, 50.
Zhang, Q.Q., Ferguson, D.K., Mosbrugger, V., Wang, Y.F., Li, C.S., 2012. Vegetation and climatic changes of SW China in response to the uplift of Tibetan Plateau. Palaeogeogr. Palaeoclimatol. Palaeoecol. 363–364, 23–36.